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How Spiders Make a Living

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ABSTRACT Although the beneficial status of the spiders as insectivores has been widely recognized for quite some time, biologists by and large seem to be rather unfamiliar with the specific feeding habits of this very diverse order. We present an overview of the feeding patterns of 10 groups of common agroecosystem spiders to inform entomologists and ecologists concerned with issues of natural biological control. The various spider groups discussed in this article exhibit a very diverse range of life styles and foraging modes, which is reflected in the diversity of their feeding patterns. Implications of the insectivorous activities of these predators for natural pest control are discussed.

KEY WORDS spiders, predation, diets

SPIDERS (ARANEAE) ARE a very diverse order of ubiquitous carnivores within the class Arachnida. At the present time, >30,000 species of spiders are described (Coddington & Levi 1991). Over 3,000 species occur in North America alone (Young & Edwards 1990). The vast majority of spiders occupy terrestrial habitats. Some lycosids and pisaurids, however, can walk and *sail* on the water surface (and at times even dive and swim under water); they forage on aquatic and semiaquatic organisms when they inhabit marshes, flooded rice fields, and other wetlands (Greenstone 1979, Oraze & Grigarick 1989, Zimmermann & Spence 1989). One agelenid species (the *water spider*) actually lives under water (see subsection *Foraging Patterns of Web Weavers*). Most spiders are highly cannibalistic solitary creatures and practice bizarre courtship rituals (Turnbull 1973). Several species produce sounds (acoustic communication) during courtship and agonistic displays (Rovner 1975, Uetz & Stratton 1982). These animals live in a world full of vibrations (e.g., Rovner & Barth 1981). Sexual dimorphism occurs in many species, the female normally being significantly larger than the male (hereafter *adult length* always refers to the female). Spiders disperse by walking on the ground, by using silk-thread bridges between plants, as well as *ballooning* through the atmosphere from place to place on silken threads (Foelix 1982, Dean & Sterling 1985, Young & Edwards 1990). All spiders produce silk from abdominal glands though only the *web weavers* construct webs that are used to catch prey. Spiders are equipped with a pair of jaws (chelicerae) and possess venom glands (exception, Uloboridae do not produce venom). Immobilization of prey is assisted by the use of silk and by the injection of venom. These animals cannot ingest solid food and must, therefore, inject digestive enzymes into the immobilized prey (external digestion) and then suck in the dissolved tissue in liquid form. Spiders generally have a very low rate of metabolism compared with other poikilothermic organisms of comparable body weight (Greenstone & Bennett 1980). They can store energy and starve for considerable time periods, which makes them excellent survivors under conditions of food shortage (see Nyffeler & Breene 1990a).

According to traditional foraging theory, spiders are considered to be predators of live, moving prey only (e.g., Turnbull 1960, 1973). More recent studies have modified this view when evidence was found that spiders utilize a much broader range of foraging strategies, including feeding on arthropod eggs (oophagy), dead animals (scavenging), plant pollen, and even artificial diets (see McDaniel & Sterling 1982, Nyffeler et al. 1990a). Stealing of prey from other spiders (kleptoparasitism) plays an important role as an alternative foraging strategy of various web spinners (Vollrath 1987). Spiders have been reported feeding on a wide range of different animal groups including some unusual prey such as small mice, bats, birds, fish, crayfish, crabs, frogs, lizards, snakes, and scorpions (Nyffeler & Benz 1981, McCormick & Polis 1982); however, in general they tend to concentrate on insect prey and to a lesser degree on other spiders (Wise 1993). Most spider species forage on multiple prey species (generalist predators), which Greenstone (1979) has suggested may be advantageous by optimizing a balanced essential amino acid composition in the diet. Spiders feed predominantly on small-sized prey relative to their own size (prey length ≤ predator length) (Nyffeler & Benz 1981, Wise 1993); feeding ex-

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periments with a variety of spider species and a model prey (crickets) conducted in the laboratory revealed that the optimal prey length ranges from 50–80% of the spider length (Nentwig 1987).

Spiders are among the numerically dominant insectivores in terrestrial ecosystems and exhibit a very diverse range of life styles and foraging behaviors (Turnbull 1973, Wise 1993). Two basic groups of foraging strategies can be distinguished: (1) *web spiders* (i.e., foraging with a catching web) (Tables 1–5), and (2) *hunters* or *wanderers* (i.e., foraging without the use of a web) (Tables 6–9). Some prominent representatives of web spinning spiders are orb weavers (Araneidae and Tetragnathidae), sheet web weavers (Linyphiidae), mesh web weavers (Dictynidae), comb-footed spiders (Theridiidae), and funnel-web weavers (Agelenidae). Prominent representatives of hunters are wolf spiders (Lycosidae), lynx spiders (Oxyopidae), crab spiders (Thomisidae), and jumping spiders (Salticidae). These 10 families are among the most abundant spider predators in agroecosystems (e.g., Whitcomb 1974, Luczak 1979, Nyffeler 1982, Dean & Sterling 1987); and because of their high colonization power and insectivorous feeding behavior, they are of interest to the entomologist and ecologist concerned with issues of natural biological control (compare Turnbull 1973, Riechert & Lockley 1984, Nyffeler & Benz 1987, Sterling et al. 1989). In this article, we present an overview of the feeding patterns of these 10 groups of spider predators.

Materials and Methods

There are different methods to evaluate spider diets. The prey spectra of spiders can be assessed by directly collecting prey organisms or their remains from spider webs (i.e., prey analyses of web weavers) (Tables 1–5), or collecting spiders with prey in their chelicerae in the field (i.e., prey analyses of hunters) (Tables 6–9). Spider predators (along with their prey) are placed in 70% ethyl alcohol and later identified in the laboratory, using a dissecting microscope (see Nyffeler et al. [1987b, 1989] for details). Additionally, sophisticated methods (e.g., release of prey radiolabeled with ^{32}P, ELISA techniques, chromatography) are used to detect feeding on insect eggs, tiny aphids, and mites, and other *hidden* predation activities that may otherwise be overlooked with visual observation methods (Greenstone 1979, McDaniel & Sterling 1982, Nyffeler et al. 1990a). The prey spectra presented in this article (Tables 1–9) are all based on observational data from field studies previously published in literature (see references in tables); a large portion of this information had been collected in the course of research projects conducted at Texas A&M University and the Swiss Federal Institute of Technology, respectively.

Results and Discussion

Foraging Patterns of Web Weavers. High feeding frequencies (up to 90% spiders feeding simultaneously during peak activity) were observed in field populations of certain larger-sized orb weavers (Araneidae) that rebuild (recycle) their webs daily (Nyffeler 1982). The high feeding frequencies indicate that the web is a very efficient prey capturing device. Large orb weavers often kill prey in excess of their energy requirements. As many as 1,000 small insects have been found entangled at one time in a single orb web; however, not all insects caught by the web are eaten. Sheet-web weavers, mesh web weavers, comb-footed spiders, and funnel-web weavers that do not renew their nets daily, feed less frequently (<10% spiders feeding simultaneously) (M.N. & Benz 1988a; unpublished data). Relatively low feeding frequencies were also observed in small orb weavers that spin small delicate nets (LeSar & Unzicker 1978, Culin & Yeargan 1982, Nyffeler 1982). The designs and functions of different types of spider webs are discussed explicitly by Eberhard (1990).

Orb Weavers. Orb weavers (Araneidae and Tetragnathidae) spin spiraling sticky webs on and between plants in a wide variety of field crops and natural habitats. Many orb weavers spin their webs preferentially at the beginning or end of the nocturnal period (Foelix 1982). Orb weavers wait in a head-down position for prey in the web center (hub) or in a retreat connected to the hub by a signal line. Alerted by the vibrations of an insect struggling in the web, the spider rushes to its victim; subsequently, the prey is wrapped in silk followed by a venomous bite (in some cases, the prey is first bitten and then wrapped) (Foelix 1982). The immobilized prey is later carried to the hub or retreat where it is eaten. *Tetragnatha laboriosa* Hentz (Tetragnathidae), a slender elongate orb weaver (≈6 mm adult length) of yellowish color with a silvery abdomen, is one of the most abundant spider predators of field crops in the United States (Young & Edwards 1990). With their fragile webs (≈10–15 cm in diameter) oriented at various angles, these spiders trap small soft-bodied insects predominantly of the orders Diptera and Homoptera (Table 1). Leafhoppers (Cicadellidae) represented an essential component (>30% of total) in the prey of *T. laboriosa* in soybean fields in Illinois and Kentucky (Table 1) (LeSar & Unzicker 1978, Culin & Yeargan 1982). In a cotton field in Texas, the prey of this species was composed largely of aphids (75% of total) (Table 1; Nyffeler et al. 1989). Coleoptera are often excluded as prey of small orb weavers (≤5% of total prey) (Table 1). *T. laboriosa* was seen eliminat-

Table 1. Prey spectrum (in percent) of small orb-weaver, *Tetragnatha laboriosa* Hentz (Tetragnathidae), based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	40.5	17.5	12.2
Cicadellidae	36.7	50.0	7.3
Aphididae	0.0	12.5	78.0
Other Homoptera	1.3	7.5	0.0
Heteroptera	17.7	2.5	0.0
Coleoptera	0.0	5.0	0.0
Formicidae	2.6	2.5	2.5
Lepidoptera	0.0	2.5	0.0
Others	1.2	0.0	0.0
Total	100.0	100.0	100.0
No. prey records	79	40	41

[a] In soybeans in Illinois (LeSar & Unzicker 1978).
[b] In soybeans in Kentucky (Culin & Yeargan 1982).
[c] In cotton in Texas (Nyffeler et al. 1989).

ing entangled beetles from the web by the following tactics: (1) by the spider violently shaking the web until the beetle fell, (2) by ignoring the beetle until it worked itself free and could escape, (3) by cutting the web around an adult beetle allowing it to drop from the web (LeSar & Unzicker 1978, Culin & Yeargan 1982). Fragile, small nets of small orb weavers such as *T. laboriosa* are suitable for interception of small insects only (narrow feeding niche) (LeSar & Unzicker 1978, Culin & Yeargan 1982).

In contrast, large orb weavers of the family Araneidae are able to overcome the defenses of a wider diversity of prey types, with their strong nets (broad feeding niche), which include insects with strong sclerotization, chemical protection, and aggressive behavior (Culin & Yeargan 1982, Nentwig 1987). Large orb weavers of the genus *Argiope* frequently kill grasshoppers (Orthoptera) and large stinging bees (including *Apis mellifera* L.) (Table 2; Nyffeler & Breene 1991). Grasshoppers (genera *Melanoplus*, *Encoptolophus*, and *Schistocerca*) constituted 18% of the total prey intercepted in the ≈30 cm diameter webs of *Argiope aurantia* Lucas in a cotton field of East Texas (Table 2); this spider (≈20–25 mm adult length) kills prey up to ≈200% of its own size (Nyffeler et al. 1987a).

Table 2. Prey spectrum (in percent) of large orb-weavers (Araneidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	26.8	77.8	69.2
Aphididae	30.0	0.0	11.1
Orthoptera	17.9	12.2	0.1
Apis mellifera L.	1.1	4.4	15.5
Other Apidae	2.1	0.0	0.0
Formicidae	8.4	0.0	0.0
Other Hymenoptera	1.0	0.0	2.2
Coleoptera	5.8	1.1	0.0
Araneae	0.0	3.3	0.0
Lepidoptera	0.0	0.0	0.0
Others	6.9	1.2	1.9
Total	100.0	100.0	100.0
No. prey records	190	90	215

[a] *Argiope aurantia* Lucas in cotton in Texas (Nyffeler et al. 1987a).
[b] *Argiope bruennichi* (Scopoli) in grassland in Switzerland (Nyffeler 1982).
[c] *A. bruennichi* in grassland in Switzerland (Nyffeler 1982).

Orb weavers generally seem to be rather ineffective in trapping moths and butterflies. Eisner et al. (1964) stated: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and fly on." Nyffeler (1982) recorded that flying lepidopterans made up a very low percentage of the prey of various temperate orb weaver species. Several species of orb weavers, however, spin highly modified orb webs (e.g., *ladder web* and *bolas spider*) that function as effective moth traps (Foelix 1982, Eberhard 1990).

Sheet-Web Weavers. The family of sheet-web weavers (Linyphiidae) includes the subfamilies Linyphiidae-Linyphiinae and Linyphiidae-Erigoninae (=Erigonidae or Micryphantidae). These spiders hang inverted below the sheet waiting for prey, which they pull through the sheet (Wise 1993). Linyphiid webs include some viscid silk though it does not seem to be much involved in prey capture. Various small to medium-sized species of the subfamily Linyphiinae can reach high abundance in woodlands and grasslands where they kill numerous small insects primarily from the orders Diptera, Hymenoptera, Homoptera, and Heteroptera (Turnbull 1960, Nyffeler & Benz 1981). Lepidopterans and coleopterans often escape from the fragile sheet webs and, thus, compose an insignificant fraction of these spiders' diet (Turnbull 1960). Dwarf spiders of the subfamily Erigoninae (*Erigone* spp. and *Oedothorax* spp.), <3 mm in length, numerically dominate the spider faunas on the ground surface of agricultural fields in the temperate-northern zones (Sunderland et al. 1986, Nyffeler & Benz 1988a). With fragile small sheet webs spun horizontally over small depressions on the ground, these tiny spiders capture small soft-bodied insects, including numerous springtails (Collembola), dipterans, and homopterans (Table 3). Agriculturally harmful cereal aphids can form a significant portion (≈12–40%) in the prey of the dwarf spiders in European winter wheat fields (Table 3) (Sunderland et al. 1986, Nyffeler & Benz 1988a). Green rice leafhoppers, *Nephotettix cincticeps* (Uhler), and brown planthoppers, *Nilaparvata lugens* (Stal), composed ≈60% of the prey of *Oedothorax insecticeps* Boes. & Str. in rice fields in Asia (Table 3; Kiritani et al. 1972).

Mesh-Web Weavers. Mesh-web weavers (Dictynidae) are small spiders (≤3 mm in length) of brownish, greyish, or green color that use the

Table 3. Prey spectrum (in percent) of sheet-web weavers (Linyphiidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Nilaparvata lugens (Stal)	0.0	0.0	23.9
Nephotettix cincticeps (Uhler)	0.0	0.0	38.9
Aphididae	38.7	12.1	—[d]
Collembola	37.8	71.7	—[d]
Diptera	13.5	5.6	—[d]
Thysanoptera	—[d]	4.0	—[d]
Araneae	0.0	1.5	16.3
Others	10.0	5.1	20.9
Total	100.0	100.0	100.0
No. prey records	111	198	226

[a] *Erigone* spp./*Oedothorax* spp. in winter wheat in Switzerland (Nyffeler & Benz 1988a).

[b] Various linyphiid species in winter wheat in England (Sunderland et al. 1986).

[c] *Oedothorax insecticeps* Boes. & Str. in rice fields in Japan (Kiritani et al. 1972).

[d] Information not available.

Table 4. Prey spectrum (in percent) of comb-footed spiders (Theridiidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Solenopsis invicta (Buren)	0.0	75.3	0.0
Other Formicidae	92.0	0.4	0.0
Coleoptera	0.0	15.1	3.1
Diptera	0.0	0.0	27.8
Aphididae	0.0	4.6	42.6
Cicadellidae	3.0	0.8	0.0
Thysanoptera	0.0	0.0	9.0
Ephemeroptera	0.0	0.0	7.6
Others	5.0	3.8	9.9
Total	100.0	100.0	100.0
No. prey records	101	258	223

[a] *Achaearanea riparia* (Blackwall) under overhanging grass in Switzerland (Nyffeler & Benz 1981).

[b] *Latrodectus mactans* (F.) in cotton in Texas (Nyffeler et al. 1988).

[c] *Theridion impressum* L. Koch in wheat fields in Switzerland (Nyffeler 1982).

calamistrum to comb out *cribellate silk* from a sieve-like plate just forward of the other spinnerets called the cribellum. Soft-bodied insects, predominantly small adult dipterans and homopterans, are intercepted in the small irregular mesh webs that the dictynids spin on leaves of various field crops and wild plants (Nyffeler & Benz 1981, Nentwig 1987). Agriculturally harmful dipterans and aphids can compose a high percentage in the diet of dictynid spiders (Heidger & Nentwig 1989). In other studies, dictynids were recorded foraging on small bugs (Heteroptera) (Nyffeler et al. 1992b).

Comb-Footed Spiders. This family (Theridiidae) of small to medium-sized species, are characterized by a globular abdomen. Theridiids spin irregular webs and throw viscid silk on their victim before biting it (Nentwig 1987). Theridiids are, in general, exceedingly polyphagous (Nyffeler & Benz 1981). However, in environments where ants occur in large numbers, these spiders can switch to predominantly feeding on ants (myrmecophagy; Table 4) (MacKay 1982, Nyffeler et al. 1988). Ants compose >90% of the prey of the European species *Achaearanea riparia* (Blackwall) (≈3.5 mm adult length) under overhanging grass (Table 4). Myrmecophagy was also observed in the southern black widow spider, *Latrodectus mactans* (F.), a dangerously venomous species whose black colored females (≈10 mm in length) show a distinct red hourglass marking on the ventral part of the abdomen. *L. mactans* was observed to capture primarily red imported fire ants, *Solenopsis invicta* (Buren), (75% of total prey; Table 4) in cotton fields of East Texas, where this spider builds irregular mesh type webs in holes in the ground, in large depressions between dirt clods on the ground surface, or in the lowest branches of plants (Nyffeler et al. 1988). Black widow immatures, third instar or older, can capture fire ant workers. Black widow spiders also frequently capture beetles (15% of total prey; Table 4) including the boll weevil, *Anthonomus grandis grandis* Boheman (Whitcomb 1974, Nyffeler et al. 1988). The western widow spider, *Latrodectus hesperus* Chamberlin & Ivie, known to feed primarily on various beetles (Pratt & Hatch 1938), was observed foraging on harvester ants in California (MacKay 1982). Some theridiids (*Steatoda* spp. with ≈6 mm adult length) feed primarily on a diet of various flies and meal-infesting insects in stables and barns (Nyffeler & Benz 1987). Aphids constituted ≈10–90% of the prey of theridiids in European field crops (Nyffeler & Benz 1981).

Small kleptoparasitic theridiids, *Argyrodes* spp. (≈4 mm adult length), live in the webs of other spider species and forage by stealing prey from the host or taking prey below the threshold of acceptability (in size) of the host, or occasionally attacking the host or its young (Nyffeler et al. 1987a, Vollrath 1987).

Funnel-Web Weavers. These weavers (Agelenidae) trap their prey by means of funnel-like sheet webs. At the entrance of the funnel, the spider waits for prey. When an insect lands on the sheet, the spider runs quickly to the victim, bites it, and carries it to the funnel entrance where feeding takes place. Mass occurrences of *Agelena labyrinthica* (Cl.), a dark brown European species, with ≈10 mm adult length, can sometimes be seen in minimally disturbed grassland (old fields). In the strong extensive funnel webs, these spiders capture a wide variety of different insect groups (Table 5), which includes at times numerous agriculturally harmful lepidopterans from the family Pieridae. Honey bees, *A. mellifera,* and grasshoppers (Orthoptera) constitute high proportions in the prey of this spider in some habitats (Table 5; Nyffeler 1982).

In the litter of European woodlands, the dark brown *Coelotes terrestris* (Wider) (≈10 mm

Table 5. Prey spectrum (in percent) of funnel web-weavers (Agelenidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Apis mellifera L.	23.3	1.9	0.0
Formicidae	13.3	5.7	1.0
Other Hymenoptera	8.3	1.9	1.0
Orthoptera	0.0	26.4	0.0
Coleoptera	5.0	7.5	64.0
Lepidoptera	18.3	37.7	0.0
Diptera	11.7	15.1	17.0
Trichoptera	10.0	0.0	0.0
Dermaptera	0.0	0.0	8.0
Other	10.1	3.8	9.0
Total	100.0	100.0	100.0
No. prey records	60	53	306

[a] *Agelena labyrinthica* (Cl.) in grassland in Switzerland (Nyffeler 1982).
[b] *A. labyrinthica* in grassland in Switzerland (Nyffeler 1982).
[c] *Coelotes terrestris* (Wider) in hedges in Germany (Petto 1990).

adult length) builds tube-like funnels that end several centimeters under ground. Most of the remains found in such ground funnels were the elytra of beetles (including numerous Carabidae), which indicates that *C. terrestris* concentrates largely on beetle prey (Table 5; Nyffeler & Benz 1981, Petto 1990). The hard-sclerotized beetles are probably not optimal diet for most smaller-sized spiders, because the chelicerae cannot penetrate the thick cuticle of these insects (Nentwig 1987). Some spider species, which inhabit microhabitats rich in beetle prey such as *C. terrestris*, exhibit a specialized predatory behavior by biting into the intersegmental membranes of beetles (Nentwig 1987). Spiders that live in tubes under ground, e.g., Atypidae, Ctenizidae, and Eresidae (≈10–15 mm in length), concentrate largely on beetle prey (Nyffeler & Benz 1981).

Another agelenid, the water spider *Argyroneta aquatica* Clerck (≈10 mm adult length), lives in a bell (air bubble attached to water plant) under water in ponds and streams. This palaearctic species mostly hunts fly larvae and small crustaceans (Foelix 1982). (Recently *Argyroneta* has been placed into its own family, Argyronetidae [Platnick 1993]).

Foraging Patterns of Hunters. Low feeding frequency (≤10% spiders feeding simultaneously in a given population) was observed in each of the four families of hunters described in this article (wolf spiders, lynx spiders, crab spiders, and jumping spiders) (Nyffeler & Breene 1990a). With a visual method based on average percentage of spiders with prey in their chelicerae observed in the field, average hunting (searching) time, and handling time assessed in the laboratory, the predation rate (number of prey per spider per day) of a spider individual can be roughly estimated (Nyffeler et al. 1987b). With this method we estimated that adult wolf spiders and lynx spiders may capture an average of ≈1 prey per spider per day in the field (Nyffeler & Benz 1988b, Nyffeler et al. 1992a). Field populations of hunting spiders were observed in an underfed condition by researchers in North America, Europe, and Japan (see Nyffeler & Breene [1990a] for a review). Apparently, low feeding frequency is a pattern characteristic for spiders foraging without a web in the natural environment (Zimmermann & Spence 1989, Wise 1993). Significantly higher feeding frequencies can be observed in laboratory experiments when food is offered ad libitum (Nyffeler & Breene 1990a, Nyffeler et al. 1992a). High levels of cannibalism, observed in hunting spiders, may be crucial for their survival under conditions of food limitation.

Wolf Spiders. These spiders (Lycosidae) are small to large-sized animals, characterized by the specific arrangement of their eight eyes; they form three rows with the anterior row consisting of four small eyes and the two back rows consisting each of two larger eyes. These spiders are vagrant hunters that forage on the ground surface well-camouflaged by their brownish to greyish coloration. Contrary to common belief, wolf spiders do not necessarily run down their prey (Wise 1993). More recent studies suggest that they tend towards a *sit-and-wait* foraging strategy. With their stout chelicerae they chew down their prey to a "meat ball" (Kiritani et al. 1972). Wolf spiders of the genus *Pardosa* (5–8 mm adult length) are often characterized as diurnal foragers (e.g., Yeargan 1975); but nocturnal predation activities could be monitored as well (Whitcomb 1974, Hayes & Lockley 1990). *Pardosa* spp. wolf spiders are abundant in field crops, grasslands, and woodlands where they forage on small soft-bodied arthropods. Their diet includes springtails (Collembola), small dipterans, and homopterans (Table 6; Edgar 1970, Nyffeler & Benz 1988b, Nyffeler & Breene 1990a). Agriculturally harmful cereal aphids can constitute an essential portion in the diet of *Pardosa* spp. in European winter wheat fields (Table 6; Nyffeler & Benz 1988b). Leafhoppers and dipterans constitute essential components in the diet of *Pardosa ramulosa* (McCook) in field crops in California (Table 6; Yeargan 1975, Oraze & Grigarick 1989). In rice fields in Asia, green rice leafhoppers, *N. cincticeps*, and brown planthoppers, *N. lugens*, composed ≈80% of the diet of wolf spiders (Table 6; Kiritani et al. 1972). Mosquitoes (*Aedes*), shore flies (*Ephydra*), and bugs (waterboatman *Trichocorixa*) are the primary food source for *P. ramulosa* in marshes (Greenstone 1979).

Large nocturnal wolf spiders, genera *Rabidosa* and *Hogna* (previously known as *Lycosa*, ≈15–20 mm adult length), often feed on bulky prey including large grasshoppers, crickets, bee-

Table 6. Prey spectrum (in percent) of wolf spiders (Lycosidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Nilaparvata lugens (Stål)	0.0	0.0	24.9
Nephotettix cincticeps (Uhler)	0.0	0.0	52.6
Other Cicadellidae	0.0	19.3	—[d]
Aphididae	27.1	4.8	—[d]
Diptera	27.1	22.1	—[d]
Collembola	25.4	1.8	—[d]
Heteroptera	0.0	11.5	—[d]
Orthoptera	0.0	6.3	—[d]
Coleoptera	5.1	6.0	—[d]
Araneae	6.8	19.6	8.9
Others	8.5	8.6	13.6
Total	100.0	100.0	100.0
No. prey records	59	331	1,553

[a] *Pardosa* spp. in winter wheat in Switzerland (Nyffeler & Benz 1988b).

[b] *Pardosa ramulosa* (McCook) in alfalfa fields in California (Yeargan 1975).

[c] *Pardosa* (=*Lycosa*) *pseudoannulata* (Boes. & Str.) in rice fields in Japan (Kiritani et al. 1972).

[d] Information not available.

tles, noctuid moths, and other spiders (Van Hook 1971, Whitcomb 1974, Hayes & Lockley 1990).

Lynx Spiders. These predators (Oxyopidae) are characterized by the erect long spines on their legs and by a hexagonal eye arrangement. Lynx spiders can be active day or night (Nyffeler et al. 1987b). The striped lynx spider, *Oxyopes salticus* Hentz, a light-colored species with an average adult length of ≈6 mm, was found to be the most abundant spider predator in cotton fields and other agricultural crops in parts of the southern United States (Dean & Sterling 1987, Young & Edwards 1990). *O. salticus* is a pouncing hunter that actively searches the plant surface for prey. This spider captures a wide variety of small-sized arthropods (up to ≈6 mm maximum prey length) and shows considerable flexibility in switching its dietary composition in response to prey availability (Table 7). Small bugs (Heteroptera) apparently are optimal diet for *O. salticus* (Lockley & Young 1987; Agnew & Smith 1989; Breene et al. 1990; Nyffeler et al. 1992a, b). Lockley & Young (1987) reported that *O. salticus* fed heavily on tarnished plant bugs, *Lygus lineolaris* (P. de B.) (40% of total prey), cotton fleahoppers, *Pseudatomoscelis seriatus* (Reuter) (8%), and other bugs (6%) in a cotton field in Mississippi (Table 7). In a cotton agroecosystem in Texas, *O. salticus* preyed heavily on cotton fleahoppers (24% of total prey; Table 7), but in another cotton area with low incidence of fleahoppers and other *true* bugs, red imported fire ants (*S. invicta*) were most frequently captured (22% of total prey; Table 7) (Nyffeler et al. 1987b, 1992a).

Table 7. Prey spectrum (in percent) of lynx spider, *Oxyopes salticus* Hentz (Oxyopidae), based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Pseudatomoscelis seriatus (Reuter)	8.3	23.8	0.0
Lygus lineolaris (P. de B.)	39.6	1.6	0.0
Other Heteroptera	6.2	9.5	4.7
Diptera	18.7	15.9	17.2
Aphididae	0.0	12.7	14.1
Cicadellidae	16.7	0.0	17.2
Solenopsis invicta (Buren)	0.0	9.5	21.9
Lepidoptera	6.2	0.0	0.0
Araneae	0.0	15.9	14.1
Others	4.3	11.1	10.8
Total	100.0	100.0	100.0
No. prey records	48	63	64

[a] In cotton in Mississippi (Lockley & Young 1987).

[b] In cotton in Central Texas (Nyffeler et al. 1992a).

[c] In cotton in East Texas (Nyffeler et al. 1987b).

Pollinating bees attracted to wild flowers and cotton plants during bloom are frequently encountered and overpowered by the green lynx spider *Peucetia viridans* (Hentz), a larger sized aggressive species (up to >15-mm length), that lies in ambush on the upper surface of leaves well camouflaged by its bright green color and cryptic posture. Bees (including *A. mellifera*) constituted 23% of the prey of green lynx spiders in a Texas cotton field; these spiders also prey on pests such as cotton fleahopper and boll weevil (Nyffeler et al. 1992a).

Crab Spiders. These spiders (Thomisidae) are a family of small to medium-sized species of spiders characterized by their crab-like posture and walking behavior (like crabs they walk laterally). Crab spiders are among the most abundant spider predators in grasslands and agricultural crops. They are considered to be typical sit-and-wait foragers that lie motionless in ambush for prey. McDaniel & Sterling (1982), however, provided evidence that crab spiders may at times actively search for prey (feeding on immobile insect eggs). Feeding can take place day or night. Brown colored crab spiders of the genus *Xysticus* (≈7 mm adult length) feed on small winged Hymenoptera and Diptera most frequently when observed on meadow plants (Table 8); those on the soil surface prey more often on ants, spiders, carabid beetles, and springtails (Table 8; Nyffeler & Breene 1990b). Early-instar crab spiders feed on soft-bodied insects such as tiny dipterans, hymenopterans, aphids, and thrips, whereas later instars and adults occasionally overpower large and well-armed insects including large stinging bees. Large bees comprised <5% of the total prey of *Xysticus* spp. in hay meadows (Nyffeler & Breene 1990b). Morse's (1983) quantitative prey analysis listed large bees (*A. mellifera, Bombus* spp.) as comprising ≈50% (by numbers) of the natural diet of *Misumena vatia* (Clerck) (Table 8). This white, yellow, or pale green colored spider of ≈10 mm adult length is perfectly camouflaged on flowers where it waits in ambush for pollinating insects. *Misumenops celer* (Hentz) (≈6 mm adult length)

Table 8. Prey spectrum (in percent) of crab spiders (Thomisidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	64.8	0.0	7.0
Apidae	4.0	0.0	49.3
Formicidae	4.8	34.3	—[d]
Other Hymenoptera	8.0	2.9	4.2
Lepidoptera	1.6	0.0	29.6
Coleoptera	4.8	8.6	—[d]
Aphididae	0.0	11.4	—[d]
Collembola	0.0	5.7	—[d]
Araneae	6.4	25.7	—[d]
Others	5.6	11.4	9.9
Total	100.0	100.0	100.0
No. prey records	125	35	71

[a] *Xysticus* spp. on meadow plants in Switzerland (Nyffeler 1982).
[b] *Xysticus* spp. on soil surface of meadows in Switzerland (Nyffeler 1982).
[c] *Misumena vatia* (Clerck) on flowers in Maine (Morse 1983).
[d] Information not available.

feeds readily on various bugs in field crops (Dean et al. 1987, Agnew & Smith 1989, Breene et al. 1990). Crab spiders were reported feeding on the Colorado potato beetle (Cappaert et al. 1991).

Jumping Spiders. This is a family (Salticidae) of small to large-sized species with rectangular shape, short stout legs, and greatly enlarged anterior median eyes. Possessing acute vision these diurnal hunters react to visual stimuli such as passing insects (Foelix 1982). They crawl to within striking distance and then jump on their prey with great accuracy. Spiders of this family are highly polyphagous (Table 9) but can narrow their prey spectrum significantly, when a suitable prey species reaches high numbers relative to other prey groups. A form of facultative monophagy was observed in the jumping spider *Plexippus paykulli* (Audouin), a cosmopolitan species of ≈10 mm adult length, that takes up residence in and on buildings and rarely migrates into field crops. This species is known from the literature as a polyphagous feeder on a wide variety of arthropod taxa including Odonata, Orthoptera, Homoptera, Lepidoptera, Diptera, Hymenoptera, and other Araneae (Jackson & MacNab 1989, Nyffeler et al. 1990b). However, in a roach-infested building in Central Texas this spider was observed to concentrate largely on the German cockroach, *Blattella germanica* (L.), as a food source (>90% of total prey; Table 9); regardless of the highly limited diet, the *P. paykulli* females produced viable offspring, which implies that the nutritional quality of the food supply was sufficient for the spiders' growth and reproductive needs (Nyffeler et al. 1990b).

Table 9. Prey spectrum (in percent) of jumping spiders (Salticidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Blattella germanica (L.)	0.0	0.0	96.4
Pseudatomoscelis seriatus (Reuter)	44.4	0.0	0.0
Lygus lineolaris (P. de B.)	0.0	22.4	0.0
Other Heteroptera	2.8	8.6	0.0
Diptera	2.8	12.1	0.0
Cicadellidae	5.6	0.0	0.0
Membracidae	0.0	15.5	0.0
Hymenoptera	8.3	1.7	0.0
Lepidoptera	8.3	1.7	0.0
Coleoptera	0.0	22.4	0.0
Orthoptera	5.6	0.0	3.6
Araneae	22.2	15.5	0.0
Others	0.0	0.0	0.0
Total	100.0	100.0	100.0
No. prey records	36	58	28

[a] *Phidippus audax* (Hentz) on wild plants and cotton in Texas (Dean et al. 1987 and M.N. unpublished data).
[b] *P. audax* on wild plants and cotton in Mississippi (Young 1989).
[c] *Plexippus paykulli* (Audouin) in building in Texas (Nyffeler et al. 1990b).

Another member of the jumping spider family, *Phidippus audax* (Hentz) (≈10 mm adult length), is one of the most abundant spider predators in field crops in the United States (Young & Edwards 1990). *P. audax* feeds heavily on agriculturally harmful bugs such as cotton fleahoppers and tarnished plant bugs (Table 9; Dean et al. 1987, Young 1989). This spider demonstrated a sigmoid functional response to the availability of fleahopper prey in field confinement tests (Breene et al. 1990). *P. audax* also preys on beetles (e.g., spotted cucumber beetle and boll weevil) and larvae of the bollworm, *Helicoverpa zea* (Boddie) (Young 1989). Jumping spiders frequently eat other spiders (Jackson 1977) (Table 9). In different parts of the world, jumping spiders were observed feeding on insect eggs (Whitcomb 1974, McDaniel & Sterling 1982, Nyffeler et al. 1990a). Some salticid species (*Portia* spp.) habitually invade the webs of other spiders and eat the web owners (araneophagy) (Jackson & Blest 1982). Members of the family Mimetidae (pirate spiders) are known to prey exclusively on other spiders in the field (Foelix 1982, Agnew & Smith 1989, Wise 1993) but in the laboratory some mimetids feed on insects as well (Nentwig 1987).

The feeding behaviors of other spider groups are discussed elsewhere (e.g., Nentwig 1987, Wise 1993). The wide variety of spider diets shown in Tables 1–9 reflects the diversity and flexibility of foraging behavioral patterns utilized by these animals in their quest for food.

Ecological Implications of the Insectivorous Activities of Spiders. As generalist predators, spiders destroy pest insects, insects of a neutral economic status, and beneficials alike (Bilsing 1920, Whitcomb 1974, Nyffeler 1982). The same spider species that feeds predominantly on pests at a certain location, may capture mostly beneficials at another location only a few kilometers away. The orb weaver *Argiope bruennichi* (Scopoli) for instance preys primarily on acridid grasshoppers in some grasslands in Central Europe; however, in small old fields dominated by flowering thistles and blackberry bushes, this spider was observed capturing large numbers of honey bees (Nyffeler & Benz 1981). Honey bees, bumble bees, and other pollinating insects are a primary food source for some aggressive spiders that search and wait for prey on or near flowering plants (see above) (Bilsing 1920, Nentwig 1987, Nyffeler & Breene 1991). Agnew & Smith (1989) and Nyffeler et al. (1987b, 1992a) observed that in field crops in the southwestern United States, spiders frequently kill and eat other predators (intraguild predation). Whitcomb (1974) stated that some web weaving spiders destroy large numbers of parasitoids and predators. These negative effects, however, are balanced by spider activities in killing numerous pest insects as well (for a discussion see Agnew & Smith [1989], Nyffeler & Breene [1991], and Nyffeler et al. [1987b, 1992a, b]). Furthermore, predation on beneficials may be helpful in maintaining the number of spiders during a period of food shortage (low pest levels).

Although the ecological significance of spiders in the balance of nature is still largely unexplored, they generally are considered to be important natural enemies of insects (Robinson & Robinson 1974, Whitcomb 1974, Zimmermann & Spence 1989, Young & Edwards 1990). Turnbull (1973) surveyed 37 published censuses of spider numbers in a wide variety of natural and modified environments. He found an overall mean density of 130.8 spiders per square meter (range, 0.6–842/m^2) and concluded that spiders must have an enormous predation impact on insect populations. Especially in minimally disturbed systems such as old fields, marshes, and woodlands colonized by spiders all year long in high numbers (up to a maximum of ≈1,000/m^2) (see Dondale 1971), these animals seem to play an important ecological role as insectivores (Nyffeler & Benz 1987). The prey kill by the spiders of such ecosystems was estimated at ≈50–200 kg fresh weight per hectare per year (Teal 1962, Kajak et al. 1971, Van Hook 1971, Stern & Kullmann 1975), which may be ≈100 times higher compared with average agricultural fields of the temperate-northern zones (Kajak et al. 1971, Luczak 1975, Nyffeler 1982) (Table 10). Nyffeler et al. (1994) surveyed 25 censuses of spider numbers in U.S. field crops published by 11 different research groups (considering a geographic range from North Carolina to California), which gave an overall mean density of ≈1 plant-dwelling spider per square meter (±0.18 SEM). Spider numbers in cotton throughout Texas averaged 0.8/m^2 (Dean & Sterling 1987). Such estimates are based on D-Vac samples, whole plant sampling, and ground cloth technique (e.g., Dean & Sterling 1987). These methods do not take into account those spiders that inhabit cracks in the soil between the rows, and the available data from field crops are, therefore, rather conservative estimates. Nevertheless, mean spider densities in U.S. crops are significantly lower than Turnbull's overall mean value of 130.8/m^2 (see above). Field crops are highly disturbed systems whose beneficial arthropod numbers are drastically reduced by agricultural practices such as frequent mowing, cultivating, combine-harvesting, and use of heavy doses of pesticides (Luczak 1979, Nyffeler 1982, Riechert & Lockley 1984).

Table 10. Prey kill of spiders in various ecosystems (rough estimates computed from literature data [modified after Nyffeler 1982])

Ecosystem	Geographic area	Prey kill kg/ha/yr
Field crops and mown meadows[a]	Central Europe	≤2
Phragmites reed belt of lake (mown once/year)[b]	Central Europe	≈5–10
Minimally disturbed grassland (old field)[c]	United States	≈50
Minimally disturbed grassland (old fields) and forests[d]	Central Europe	≈100–150
Marsh land[e]	United States	≈200
Tropical coffee plantation (insecticide-free)[f]	Oceanic-Australian region	≈160

For purposes of comparison all estimates are converted to Kilograms (freshweight)/ha/yr. Assumptions: ≈80% of the killed prey is consumed; caloric equivalent of prey is ≈5.6 cal/mg dry weight (Moulder & Reichle 1972).

[a] Kajak et al. (1971); Luczak (1975).

[b] Pühringer (1979).

[c] Van Hook (1971).

[d] Kajak et al. (1971); Stern & Kullmann (1975).

[e] Teal (1962).

[f] Robinson & Robinson (1974).

In the literature, methods by which predator numbers in an agroecosystem could be increased are discussed (Nyffeler 1982, Sterling et al. 1989, Wise 1993). Young & Edwards (1990) suggest several management strategies (e.g., reduction of pesticide usage and cultivation frequencies) that could enhance the spider numbers in field crops and adjacent habitats resulting in increased predation activities. In Japan, attempts have been made to raise the fecundity of spiders in rice fields artificially by releasing *Drosophila* flies as a supplementary food supply; this caused an increase in spider numbers (i.e., augmentation of natural enemies) (Kobayashi 1975).

There is evidence that spiders may play an important role as mortality agents of certain crop pests of small body size such as aphids (Aphididae), leafhoppers (Cicadellidae), planthoppers (Delphacidae), and fleahoppers (Miridae) in some agricultural fields where little or no insecticide is used (Kiritani et al. 1972, Liao et al.

1984, Oraze & Grigarick 1989, Nyffeler et al. 1992b). Robinson & Robinson (1974) estimated that spiders may destroy the equivalent of ≈160 kg insects per hectare per year in an insecticide-free coffee plantation in New Guinea (Table 10). These authors cautiously conclude that the absence of coffee pests in their study area may be, at least in part, attributable to the collective predation impact of the rich spider fauna. Sterling et al. (1992) demonstrated with computer modelling techniques that the insectivorous activities of spiders and other arthropod predators are of economic value in certain years in unsprayed cotton in Texas. Experimental evidence for the ecological impact of spiders has been reviewed in detail by Wise (1993) (see his book for original citations).

Coddington & Levi (1991) state that the order Araneae ranks seventh in global diversity after the five largest insect orders (Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera), and the arachnid order Acari. Wise (1993) considers the spider a 'model predator' in terrestrial ecosystems. Van Hook (1971) and other ecologists recognized that spiders as secondary consumers "may contribute significantly in maintaining community homeostasis." Spiders play an integral part in herbivore- and detritus-based food chains in terms of biomass, energy flow, and nutrient transfers (Turnbull 1973, Schoener 1989, Wise 1993). Surprisingly, the basics of spider predation ecology (i.e., prey preferences, search areas, search times, handling times, predation rates, functional and numerical responses) are still largely unknown for most species. Further detailed investigations on the predatory role and economic impact of spiders in various natural and agricultural habitats are urgently needed. With this article we hope to generate some interest among entomologists and ecologists for future studies on spider impact.

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